

FILTER FEEDING OF *SIMULIUM FULVINOTUM* (DIPTERA: SIMULIIDAE) IN THE  
CENTRAL AMAZON BASIN

Lawrence A. Lacey<sup>1</sup>

Insects Affecting Man and Animals Research Laboratory  
U. S. D. A., A.R.S., P.O. Box 14565  
Gainesville, FL 32604  
U.S.A.

Joyce M. Lacey

California Department of Water Resources  
Northern District  
2440 Main Street, P.O. Box 607  
Red Bluff, CA 96080

*Quaestiones Entomologicae*  
19: 41-51 1983

ABSTRACT

*Filter feeding of larval Simulium fulvinotum Cerqueira and Mello was studied near Manaus, Brazil, using particulate fluorescent dye in small black water streams. Transit time of particles through the midgut was 29.2 min in one stream with a current velocity of ca. 1 m/sec and 0.37 mg/l seston, but was only 26.1 min in another stream with 1.5–2.0 m/sec velocity and 2.01 mg/l seston. Penultimate instars of S. fulvinotum held the cephalic fans open for an average of 3.3 min before they were closed for removal of particles. Food of larvae included a variety of algae, detritus, bacteria and insect parts. Methods for obtaining adequate nutrition in the habitats of S. fulvinotum are: less frequent cleaning of fans, an efficient filtering mechanism, and location of larvae in swift current.*

RESUMO

*A alimentação através de filtração das larvas de Simulium fulvinotum Cerqueira e Mello foi estudada perto de Manaus, Brasil, utilizando uma tinta fluorescente em peguenos igarapês de água preta. O tempo de passagem através do intestino médio foi 29,2 min. em uma igarapé com correnteza de 1 m/seg e 0,37 mg/l de partículas em suspensão. Em outro igarapé com correnteza de 1,5–2,0 m/seg e 2,01 mg/l de particulás em suspensão, o tempo de passagem foi apenas 26,1 min. Indivíduos da penúltima etapa de S. fulvinotum mantiveram os filtros cefálicos abertos durante uma média de 3,3 min. antes de retrai-los para remover as partículas. A alimentação larval incluiu uma variedade de algas, detritos, bactérias e pedaços de insetos. As estratégias para obter nutrição adequada nos habitats de S. fulvinotum incluem movimentos mais lentos de alimentação, um mecanismo eficiente de filtração, e localização das larvas em correnteza rápida.*

Most biological research on the black flies of the Amazon Basin of Brazil has been on the adults of vector species with very little attention paid to the biology and ecology of larvae. One species which has been studied with respect to larval ecology and life history is *Simulium*

---

<sup>1</sup>Formerly with the Instituto Nacional de Pesquisas da Amazônia, Divisão de Ciências Médicas, Manaus, Brazil



Figure 1. Typical larval habitat of *Simulium fulvinitum*, Igarapé Acará Reserve Ducke, near Manaus, Brazil.

*fulvinotum* Cerqueira and Mello (1968); habitats were characterized by Dellome (1978); number of instars was determined by Gorayeb (1981); and predators of larvae were identified by Gorayeb and Pinger (1978).

Several studies have been conducted on the dynamics of filter feeding of other black fly species. Until now this aspect of the larval ecology of *S. fulvinotum* has not been investigated. In addition to providing basic information on the use of nutrients by simuliids in black water streams, information on larval feeding could also be useful when planning control of vector simuliid species in this habitat. Kershaw *et al.* (1968) and Helson and West (1978) demonstrated that particulate insecticides were active against target black flies with minimal effect on other aquatic organisms which did not filter feed. Feeding rate and retention time also will have a major influence on the efficacy of perorally active microbial control agents, such as *Bacillus thuringiensis* var. *israelensis* (Gaugler and Molloy 1980).

This paper presents information about filter feeding activity of larvae of *S. fulvinotum* in small streams near Manaus, Brazil.

### THE LARVAL HABITAT

*S. fulvinotum* larvae characteristically inhabit very swift current in small, shallow, black water streams (as defined by Sioli 1964; tannin-coloured, nutrient-poor water, draining podsols). The lip of the water drop in Figure 1 typifies the usual larval attachment site. In our study, habitats investigated were in primary and secondary forest 20–25 km northeast of Manaus, Brazil. In addition to typical larval habitats where current velocities of 1.5–2.0 m/sec (ca. 1 m<sup>3</sup>/sec discharge) were recorded, larvae were also found in one atypical stream (I) in current as low as 1 m/sec (.5 m<sup>3</sup>/sec discharge). Most streams where *S. fulvinotum* was found were heavily shaded. Stream I, however, was exposed to full sun because of recent deforestation.

Temperatures of 24.3–25.8°C and pH of 5.4–5.7 have been recorded for *S. fulvinotum* larval habitats (Cerqueira and Mello 1968, Dellome 1978). Water temperatures were 24.5–25.7°C during the course of our investigation.

### METHODS AND MATERIALS

Transit time of particles passing through the larval midgut was determined using a fluorescent dye (Hercules® Radiant Fluorescent Dye; orange WD 16).<sup>1</sup> Approximately 10 g of dye were suspended in a liter of water by vigorous shaking, then evenly poured into the river upstream of the larvae for 5–10 sec. After 10, 20, 30, and 40 min, leaves with attached larvae were carefully removed from the stream, so that larvae on adjacent leaves were not disturbed, and then stored in 70% ethanol. Ultimate larval instars were dissected to determine position of the dye plug in the midgut. Measurements of position of the dye and length of midgut were made with an ocular micrometer in a Zeiss dissecting microscope.

Gut filling times were recorded in Igarapé da Pedreira (Stream II) and Stream I. Both streams are located in the Cação Research Plantation (CEPLAC) 25 km northeast of

---

<sup>1</sup>Mention of a commercial or proprietary product does not constitute an endorsement by the U.S.D.A.

Manaus. Temperature in each was measured with a mercury thermometer. Current velocity at the surface was determined using a float and stop watch. Suspended particles were measured by taking 3 one-litre samples of water from each site and individually vacuum filtering each through previously weighed millipore cellulose filters (0.45  $\mu\text{m}$  pores, 47 mm diameter filter at  $\leq 40$  cm Hg suction). The filters were then dried for 15 hrs at 65°C. After cooling and equilibrating for 6 hrs in the same conditions under which the original filter weights were taken, they were weighed on a Mettler H 34 balance ( $\pm 0.1$  mg accuracy).

Gut contents of late instars collected from Stream I on two separate occasions were analyzed. Larvae were placed on ice soon after collecting until they were dissected in the laboratory later in the same day. The dissected food columns were teased apart in distilled water and observed with the aid of a light microscope.

Feeding behaviour was observed in Stream I by viewing the larvae through the bottom of a 600 ml glass beaker which was lowered into the stream within a few centimetres of the attached larvae.

Data about transit time of particles through the midgut were analyzed with regression analysis (least squares method). The 20 min samples for the two streams were compared using Student's t-test.

Primary cephalic fans of ultimate instar *S. fulvinothum* (preserved in 70% ethanol) were prepared for scanning electron microscopy by: dehydrating in ethanol and freon; critical point drying in freon; and gold coating. Scanning electron micrographs were made with a Hitachi H-600 electron microscope.

## RESULTS

Mean quantities of suspended particles in Streams I and II were 0.37 and 2.01 mg/liter, respectively. Stream velocities were ca 1.0 and 1.5–2.0 m/sec respectively. Temperature in both streams was 25.2°C.

Table 1. Posterior displacement of dye plug in the midgut of *Simulium fulvinothum* in Stream I (suspended particles 0.37 mg/l; velocity 1.02 m/sec).

Min. after exposure	No. larvae	Mean % displacement $\pm$ S.E.*
10	17	38.18 $\pm$ 2.01
20	13	64.38 $\pm$ 2.73
30	11	103.0* $\pm$ 1.75

\*Calculated by position of dye in mid- and hindgut.

Table 2. Posterior displacement of dye plug in the midgut of *S. fulvinotum* in Stream II (suspended particles 2.01 mg/l; velocity 1.5–2.0 m/sec).

Min. after exposure	No. larvae	Mean % displacement $\pm$ S.E.
10	16	39.75 $\pm$ 3.17
20	30	77.23 $\pm$ 2.21
30	15	completely passed

Data used to determine time for particles to pass through midguts of *S. fulvinotum* larvae from Streams I and II are presented in Tables 1 and 2. Predicted transit times for the two streams were 29.2 and 26.1 min, respectively. Displacement of dye plugs 20 min after initial exposure in the two populations was significantly different ( $p < 0.05$ ). The mean for the 30 min sample from Stream I was calculated from the position of dye in both the mid- and hindguts of 11 larvae. The low variance in position of dye plugs observed in the 10 and 20 min samples in each of the streams indicates rather uniform feeding rates at each location.

Larvae observed feeding *in situ* held the cephalic fans open for an average of  $3.3 \pm .3$  min (range: 1.8–4.8;  $n = 10$ ). Fans were held closed for between 2 and 25 sec for removal of particles.

Analysis of gut contents revealed a high percentage of algae (more than 50%) and detritus. The various algal taxa represented were: Chlorophyta (*Oedogonium* sp., *Ankistrodesmus* sp., *Cosmarium* sp. and an unidentified filamentous species); Chrysophyta (*Melosira* spp., *Tabellaria* spp., *Fragilaria* sp., *Nitzschia* sp., and several genera of unidentified pennate diatoms); and Cyanophyta (*Chorococcus* sp., *Oscillatoria* sp., *Spirulina* sp., and an unidentified filamentous species). In addition to living diatoms, many empty diatom frustules were found. Also present were unidentified bacteria, insect parts and sand.

## DISCUSSION

The dynamics of filter feeding by black fly larvae have been elucidated by a number of investigators and summarized by Wallace and Merritt (1980). Particle transit times of from 20 min to more than 24 hr have been recorded (Davies and Syme 1958, Ladle, Bass and Jenkins 1972, Mulla and Lacey 1976, Elouard and Elsen 1977, Wotton 1978, Schröder 1980b). Differences in filtering activity and transit time of particles through guts of filter-feeding species may be due to species, instar, temperature, stream velocity, parasitism, imminent pupation, and amount and dimensions of available seston (Mulla and Lacey 1976, Chance 1977, Elouard and Elsen 1977, Moore 1977b, Elsen, Quillévére and Hebrard 1978, Wotton 1978, Elsen and Hebrard 1979, Lacey and Mulla 1979, Elsen 1980, Schröder 1980 a, b). Increased stream velocity and/or additional amount of suspended matter in Stream II was responsible for the accelerated feeding rate of *S. fulvinotum* over that observed in Stream I. An even greater difference in feeding rate might be expected based on disparity of seston concentration and stream velocity between Streams I and II. Lack of exaggerated differences might be explained as a function of the inherent maximum filtering efficiency of *S. fulvinotum*. Kurtak (1978) observed a decrease in filtering efficiency (i.e., the portion of particles ingested

per larva per second relative to the total number of particles offered per fan area per second) when concentration of particles and stream velocity increased. Under laboratory conditions, Lacey and Mulla (1979) and Schröder (1980b) reported plateaus of optimal particle concentration and stream velocity for maximum ingestion rates. Beyond the optimum range, an increase in current velocity and particle concentration may result in feeding inhibition (Lacey and Mulla 1979, Gaugler and Molloy 1980).

A few ultimate instars with dark histoblasts (pharate pupae) were observed without dye plugs and with partially or completely empty midguts. Feeding had apparently ceased prior to pupation, and the gut was emptied by peristaltic action. Chance (1977) reported that *Simulium vittatum* Zetterstedt larvae may refrain from feeding for periods of 90 min or longer. In our study, the only individuals which failed to filter dye were pharate pupae.

Choice of larval habitat appears to be related to specific feeding methods for several black fly species (Carlsson *et al.* 1977, Kovachev 1979, Wotton 1979, 1980b) or at least choice of a specific habitat markedly influences type of nutrient the larvae will encounter (Maciolek and Tunzi 1968, Kurtak 1979). Selection of a habitat with an optimally high stream velocity would appear to maximize feeding rates where seston levels are as low as those found in the black water streams inhabited by *S. fulvinothum* larvae. In streams with waterfalls or other zones of very swift current, *S. fulvinothum* larvae are invariably found in the fastest current. Initial selection of these sites is apparently made by the ovipositing female (Gorayeb 1981).

Other feeding methods that would enhance ingestion would be more efficient use of the filtering mechanism and behaviour. Simuliid larvae are capable of filtering colloidal sized particles (Wotton 1976). Capture of these and other particles smaller than the spaces between the microtrichia of the cephalic fan rays is apparently aided by a mucosubstance which coats the cephalic fans (Ross and Craig 1980). A single median ray of the primary cephalic fan of *S. fulvinothum* is shown in Fig. 2. An enlargement of the middle portion of the ray (Fig. 3) shows microtrichia used for capture of fine particles. Microtrichia of *S. fulvinothum* are considerably longer than those of *S. vittatum* (D. A. Craig, personal communication), a species found in streams with moderate to high seston concentrations. Accelerated feeding rate of *S. fulvinothum* is at least partially influenced by this morphological adaptation to low seston loads. Increased surface area of the filtration mechanism of *S. fulvinothum* probably facilitates capture of a greater number of particles per unit of time.

Time spent by *S. fulvinothum* larvae with fans open is considerably greater than that reported by Kurtak (1973) and Craig and Chance (1982) for *S. vittatum*. Ostensibly *S. fulvinothum* maximizes contact of its cephalic fans with the current in compensation for a low particulate load. Craig and Chance (1982) hypothesize that larvae with less frequent mouthpart movements may filter more efficiently than those which clean their fans more often because the latter have their fans adducted (not exposed to food) for a significantly greater period of time. Rapid flicking of fans reported by other investigators was only occasionally seen during our observations. Observations were only made in Stream I because of disturbance of larvae in Stream II when they were observed from upstream. Observations from downstream were not possible because of a 2.5 m waterfall.

Gut contents of filter-feeding black fly larvae generally reflect relative abundance of nutritional materials within a particle size range that they can filter in the stream where they are located (Maciolek and Tunzi 1968, Moore 1977a, b, Wotton 1977, Kurtak 1979, Wallace and Merritt 1980). A wide variety of food types has been recorded for simuliid larvae, ranging from animal matter (Serra-Tosio 1967, Burton 1971, Disney 1971) to algae (Anderson and

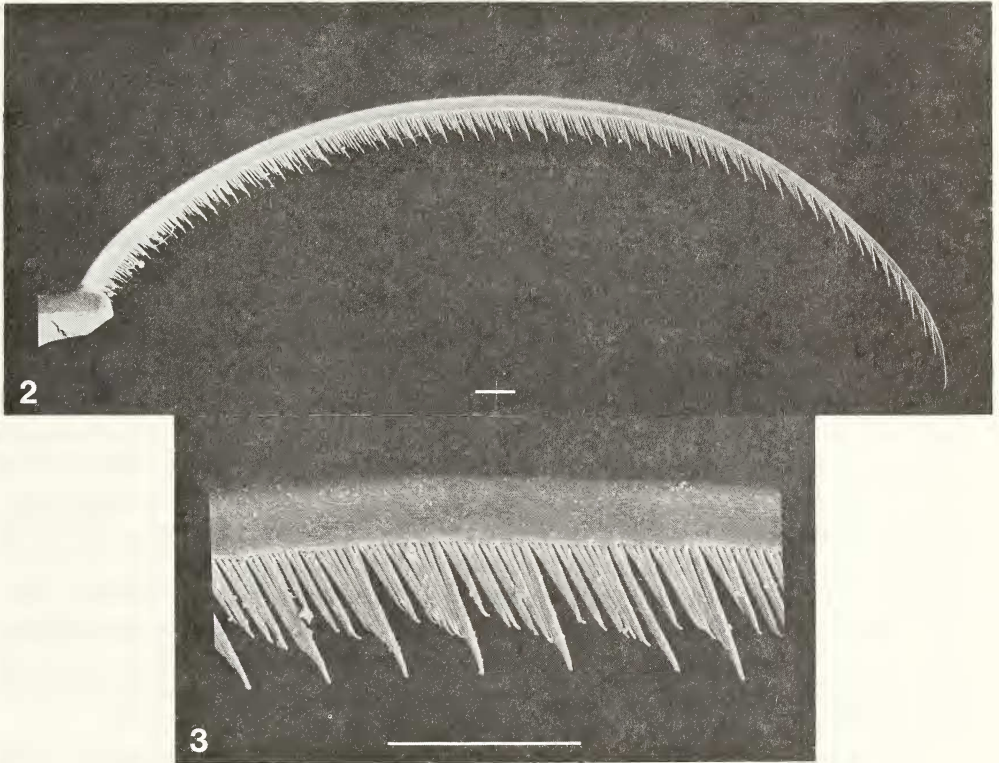


Figure 2. Middle ray of primary cephalic fan of *Simulium fulvinotum* larva.  
Figure 3. Median portion of middle ray in Figure 2. Scale = 20  $\mu$ m.

Dicke 1960, Maitland and Penney 1967, Burton 1973, Pavlichenko *et al.* 1977), bacteria (Fredeen 1964, Pavlichenko *et al.* 1977, Wotton 1980a) and detritus (Cummins and Klug 1979). Considering the low seston load, it was interesting to find algae making up the major portion of the diet of *S. fulvinothum* larvae. Algae in streams are characteristically benthic, so their contribution to the seston is generally considered to be accidental (Whitton 1975). Scraping of the substrate by *S. fulvinothum* larvae may account for the high proportion of algae in the gut. It is possible that this activity was not observed because of the low number of observations that were made *in situ*. Mokry (1975) reported that in an "average" hour, *Simulium venustum* larvae scraped for 20 min, filtered for 20 min, and rested for 20 min. Some investigators have questioned nutritional value of living algae and recently dead plant matter to larvae which have a relatively brief retention time. Kurtak (1979) and McCullough *et al.* (1979), however, reported that more than 50% of ingested diatoms were digested. Similar findings were reported by Maciolek and Tunzi (1968). In our research, the large number of empty frustules may be an indication of digestion.

Although bacteria did not appear to be a major source of food in our samples, they may be a necessary component for detritus use through biochemical alterations of the detrital substrate (Cummins and Klug 1979). Alternatively, Anderson and Cummins (1979) suggest that since retention time of food in the gut is so brief in larval simuliids, bacteria stripped from the surface of refractory detritus particles probably contribute most of the nutritional value. Lotic food sources of simuliids and their relationship with microbes are summarized by Cummins and Klug (1979).

Abundant detritus in the form of fine particulate organic matter has been associated with maintenance of dense populations of simuliid larvae (Carlsson *et al.* 1977, and other authors cited by Anderson and Seddell 1979). Detritus may have varying degrees of importance in the diet of *S. fulvinothum* larvae depending on season, location and deforestation activity. As was previously stated, most sites for *S. fulvinothum* were found under dense canopy. The site where larvae were collected for analysis of gut content was exposed to sunlight and was undoubtedly more conducive to a higher proportion of algae in the water and on the substratum. Kurtak (1979) reported variability in percentage of various food types in streams in which he worked both as a function of season and location.

The ecological role of black fly larvae, at times the most abundant aquatic insect in small streams of the Central Amazon, requires further elucidation. Areas for future research could include production studies on the larvae of *S. fulvinothum* in a wider variety of locations and seasons as well as comparison with other species of simuliids in the same general habitat. Research on the range of particle sizes ingested would be a useful first step in studying the effects of particulate insecticides on black fly larvae and nontarget organisms in the habitat of *S. fulvinothum*.

Due to its ubiquity and accessibility, *S. fulvinothum* will provide an excellent model for the study of nutrient utilization and cycling and insecticide use in the nutrient-poor black water environment.

#### ACKNOWLEDGEMENTS

The helpful comments and advice of Roger Wotton, Goldsmith's College, University of London, Douglas A. Craig, University of Alberta, and Albert Undeen, U.S.D.A., during the preparation of the manuscript are very much appreciated. We are also grateful to D. A. Craig



for making the scanning electron micrographs.

## REFERENCES

- Anderson, J. R. and R. J. Dicke. 1960. Ecology of the immature stages of some Wisconsin black flies (Simuliidae: Diptera). *Annals of the Entomological Society of America* 53: 386–404.
- Anderson, N. H. and K. W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36: 335–342.
- Anderson, N. H. and J. R. Sedell. 1979. Detritus processing by macro-invertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351–377.
- Burton, G. J. 1971. Cannibalism among *Simulium damnosum* (Simuliidae) larvae. *Mosquito News* 31: 602–603.
- Burton, G. J. 1973. Feeding of *Simulium hargeavesi* Gibbons larvae on *Oedogonium* algal filaments in Ghana. *Journal of Medical Entomology* 10: 101–106.
- Carlsson, M., M. Nilsson, Bj. Svensson, S. Ulfstrand, and R. S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. *Oikos* 29: 229–238.
- Cerqueira, N. L. and J. A. N. Mello. 1968. Simuliidae da Amazônia. IV. Descrição de *Simulium fulvinothum* sp. n. (Diptera, Nematocera). *Amazoniana* 1: 205–210.
- Chance, M. M. 1977. Influence of water flow and particle concentration on larvae of the black fly *Simulium vittatum* Zett. (Diptera: Simuliidae), with emphasis on larval filter feeding. Ph. D. dissertation. University of Alberta.
- Craig, D. A. and M. M. Chance. 1982. Filter-feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydro-dynamics. *Canadian Journal of Zoology* 60: 712–724.
- Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147–172.
- Davies, D. M. and P. D. Syme. 1958. Three new Ontario black flies of the genus *Prosimulium* (Diptera: Simuliidae) Part II. Ecological observations and experiments. *Canadian Entomologist* 90: 744–759.
- Dellome, J. 1978. Fatores físicos-químicos das criadouros de Simuliidae (Diptera: Nematocera). Master's thesis. Instituto Nacional de Pesquisas da Amazônia and Fundação Universidade do Amazonas, Manaus, Brazil.
- Disney, R. H. L. 1971. Association between black flies (Simuliidae) and prawns (Atyidae), with a discussion of the phoretic habit in Simuliids. *Journal of Animal Ecology* 40: 83–92.
- Elsen, P. 1980. Le transit intestinal chez les larves du complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. III. Influence du stade larvaire, du nycthemere et de la saison. *Annales de la Société belge Médecine tropicale* 60: 203–213.
- Elsen, P. and G. Hebrard. 1979. Le transit intestinal chez les larves du complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. II. Influence de la température de l'eau, de la concentration de particules et de la nature de ces particules. *Ibid* 59: 49–58.
- Elsen, P., D. Quillévéré, and G. Hebrard. 1978. Le transit intestinal chez les larves du

- complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. 1. Influence de sexe et de l'espèce. *Ibid* 58: 209–217.
- Elouard, J.-M. and P. Elsen. 1977. Variations de l'absorption de particules alimentaires et de la vitesse de transit digestif en fonction de certains paramètres du milieu chez les larves de *Simulium damnosum* Theobald 1903 (Diptera, Simuliidae). Cah. O.R.S.T.O.M. ser. Ent. Méd. et Parasitol 15: 29–39.
- Fredeen, F. J. H. 1964. Bacteria as food for black fly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Canadian Journal of Zoology 42: 527–554.
- Gaugler, R. and D. Molloy. 1980. Feeding inhibition in black fly larvae (Diptera: Simuliidae) and its effects on the pathogenicity of *Bacillus thuringiensis* var. israelensis. Environmental Entomology 9: 704–708.
- Gorayeb, I. S. 1981. Comportamento de oviposição e ciclo evolutivo de *Simulium fulvotum* Cerq. e Mello 1968 (Diptera, Nematocera). Acta Amazônica 11: 595–604.
- Gorayeb, I.S. and R.R. Pinger. 1978. Detecção de predadores naturais das larvas de *Simulium fulvotum* Cerq. e Mello, 1968 (Diptera, Nematocera). *Ibid.* 8: 629–637.
- Helson, B. V. and A. S. West. 1978. Particulate formulations of Abate® and methoxychlor as black fly larvicides: their selective effects on stream fauna. Canadian Entomologist 110: 591–602.
- Kershaw, W. E., T. R. Williams, S. Frost, R. E. Matchett, M. L. Mills, and R. D. Johnson. 1968. The selective control of *Simulium* larvae by paraticulate insecticides and its significance in river management. Transactions of the Royal Society of Tropical Medicine and Hygiene 62: 35–40.
- Kovachev, S. 1979. Saprobic sequences within the family Simuliidae and their importance for water quality assessment. Hydrobiology (Sofia) 9: 50–56. (In Bulgarian with Russian and English Summaries).
- Kurtak, D. C. 1973. Observations on filter feeding by the larvae of black flies (Diptera: Simuliidae). Ph. D. dissertation. Cornell University. 172 pp.
- Kurtak, D. C. 1978. Efficiency of filter feeding of black fly larvae (Diptera: Simuliidae). Canadian Journal of Zoology 56: 1608–1623.
- Kurtak, D. C. 1979. Food of black fly larvae (Diptera: Simuliidae): seasonal changes in gut contents and suspended material at several sites in a single watershed. Quaestiones Entomologicae 15: 357–374.
- Lacey, L. A. and M. S. Mulla. 1979. Factors affecting feeding rates of blackfly larvae (Diptera: Simuliidae). Mosquito News 39: 315–319.
- Ladle, M., J. A. B. Bass, and W. R. Jenkins. 1972. Studies on production and food consumption by the larval Simuliidae (Diptera) of a chalk stream. Hydrobiologia 39: 429–448.
- Maciolek, J. A. and M. G. Tunzi. 1968. Microseston dynamics in a simple Sierra Nevada lake-system. Ecology 49: 60–75.
- Maitland, P. S. and M. M. Penney. 1967: The ecology of the Simuliidae in a Scottish river. Journal of Animal Ecology 36: 179–206.
- McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. Ecology 60: 585–596.
- Morky, J. E. 1975. Studies on the ecology and biology of blackfly larvae utilizing an *in situ* benthobiosurvey. Verh. Internationale Vereinigung für Limnologie 19: 1546–1549.

- Moore, J. W. 1977a. Relative availability and utilization of algae in two subarctic rivers. *Hydrobiologia* 54: 201–208.
- Moore, J. W. 1977b. Some factors affecting algal consumption in subarctic Ephemeroptera, Plecoptera, and Simuliidae. *Oecologia* 27: 261–273.
- Mulla, M. S. and L. A. Lacey. 1976. Feeding rates of *Simulium* larvae on particulates in natural streams (Diptera: Simuliidae). *Environmental Entomology* 5: 283–287.
- Pavlichenko, V. I., A. K. Shehvenko, and M. V. Steblyuk. 1977. Study of the food spectrum of black fly larvae Diptera, Simuliidae. *Vestn. Zool* 1: 64–68. (In Russian with English summary).
- Ross, D. H. and D. A. Craig. 1980. Mechanisms of fine particle capture by larval black flies (Diptera: Simuliidae). *Canadian Journal of Zoology* 58: 1186–1192.
- Schröder, P. 1980a. Zur Ernährungsbiologie der Larven von *Odagmia ornata* Meigen (Diptera: Simuliidae). 1. Die Filtriertätigkeit unter dem Einfluss von Fließgeschwindigkeit, Wassertemperatur und Futterkonzentration. *Archiv für Hydrobiologie/Suppl.* 59: 43–52.
- Schröder, P. 1980b. Zur Ernährungsbiologie der Larven von *Odagmia ornata* Meigen (Diptera: Simuliidae). 2. Morphometrische und physiologische Bezugsgrossen, Darmentleerung und -füllzeit, Ingestion. *Ibid.* 59: 53–95.
- Serra-Tosio, B. 1967. La prise de nourriture chez la larve de *Prosimulium inflatum* Davies, 1957 (Diptera: Simuliidae). *Trav. Lab. Hydrobiol.* 57: 58: 97–103.
- Sioli, H. 1964. General features of the limnology of Amazônia. *Verh. Internationale Vereinigung für Limnologie* 15: 1053–1058.
- Wallace, J. B. and R. W. Merritt. 1980. Filter feeding ecology of aquatic insects. *Annual Review of Entomology* 25: 103–132.
- Whitton, B. A. 1975. Algae. pp 81–105 in B. A. Whitton (Ed.), *River Ecology*. University of California Press.
- Wotton, R. S. 1976. Evidence that blackfly larvae can feed on particles of colloidal size. *Nature* (London) 261: 697.
- Wotton, R. S. 1977. The size of particles ingested by moorland stream blackfly larvae (Simuliidae.) *Oikos* 29: 332–335.
- Wotton, R. S. 1978. The feeding-rate of *Metacnephia tredecimatum* larvae (Diptera: Simuliidae) in a Swedish lake outlet. *Ibid.* 32: 121–125.
- Wotton, R. S. 1979. The influence of a lake on the distribution of black-fly species (Diptera: Simuliidae) along a river. *Ibid.* 32: 368–372.
- Wotton, R. S. 1980a. Bacteria as food for blackfly larvae (Diptera: Simuliidae) in a lake-outlet in Finland. *Ann. Zool. Fennici* 17: 127–130.
- Wotton, R. S. 1980b. Coprophagy as an economic feeding tactic in blackfly larvae. *Oikos* 34: 282–286.